THE EDAPHIC FACTOR IN NARROW ENDEMISM. II. THE GEOGRAPHIC OCCURRENCE OF PLANTS OF HIGHLY RESTRICTED PATTERNS OF DISTRIBUTION

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It was my objective in the first part of this paper (4) to point out that of the three aspects of the dynamics of plant geography, namely, the environment, the physiology of the individual, and the genetics of the population, only the environmental conditions independently occupy area and hence constitute the precise determinants of particular patterns of potential area of species; and, that of environmental factors, the edaphic factor is most apt to occur in small, sharply defined areas and hence might be looked upon as a determinant of narrow patterns of endemism. We may now very briefly consider some of the aspects of the geographic pattern of restriction of plant species in nature that seem to support these conclusions. To this end we will consider especially certain cases of plants having highly restricted patterns of distribution and occurring aggregated into definite areas. We shall note further that these areas are in regions of great environmental diversity and often of local edaphic peculiarity as well.

A survey of the occurrence of highly restricted plant species throughout the world reveals that such species occur in almost all parts of the land area of the earth. However, certain regions are remarkable for the concentrations of localized species in their floras. These are frequently referred to in the literature as "endemic areas." Some of these areas rich in highly restricted endemics are on islands while others are on the continents. It is a matter of great interest that of islands rich in endemics, most, if not all, are either of volcanic origin or contain large outcrops of metamorphic rock such as gneiss, schist, chert, or serpentine in which the basic metals and other minerals occur, often over a highly localized geographic pattern. Of the islands or island groups richest in percentage of endemism in their floras, the Hawaiian Islands, St. Helena and the Canary Islands, all are of volcanic origin. New Zealand is largely volcanic or igneous and also contains considerable serpentine and other metamorphics. Madagascar has a small volcanic area and a large area of gneiss and serpentine. Corsica possesses a large expanse of folded gneiss and much serpentine containing considerable nickel. A large part of New Caledonia is serpentine containing important nickel and chromium deposits. Juan Fernandez and the Galápagos Islands are volcanic. Tasmania and Ceylon both have extensive surfaces composed of serpentines. Cuba has much ser-

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pentine and chromite. The presence of serpentine on many of these islands suggests the occurrence also of other rock containing the ferro-magnesian metals. There are probably other minerals as well that may exercise similar influences on the vegetation of these areas. The volcanic and metamorphic nature of these islands together with their montane topography suggest great environmental diversity and especially edaphic diversity. Since non-volcanic islands and islands with little or no altered rock in their surface features do not demonstrate nearly such high degrees of endemic restriction in their floras, it would seem that there must be some relationship of a cause-and-effect nature between these special geological features of vulcanism and metamorphism and the occurrence of such concentrations of endemic restriction.

In general, on the continents as on the islands, endemics are concentrated in regions noted for their great environmental diversity. On the continents the greatest environmental diversity occurs in mountainous areas, particularly in arid and semi-arid regions. Here the altitudinal effects of climate and such special features as rain shadows, wind gaps, cold-air drainage, and slope exposure serve to multiply habitats caused by diversity of an edaphic nature resulting from such forces as orogenic diastrophism, vulcanism, igneous intrusion, and alteration through metamorphism. Weathering of the type characteristic of arid regions usually results in highly mineralized soils. Under these climatic conditions the leaching of soils proceeds very slowly. In mountainous areas the localization of habitats is often more pronounced on the upper slopes; as one ascends a mountain, habitats are apt to become smaller and more localized in character and area. This is especially true where the mountain has resulted from folding and faulting of strata and the subsequent erosion and dissection of the fault blocks and folds. The restriction of plants to some of these localized montane habitats on the continents frequently has led to rather unrealistic conclusions as to relict endemism on these mountains. It is often implied that the mountain was once an island, a postulate that seems unnecessary in view of the localization of the habitats on the mountain. Some continental mountains and mountain peaks have been islands and some of their plant species may date back historically to these insular times. The restriction of the species in these areas today, however, is a problem of the conditions of today's environment and the present genetic constitution of the species population. Such conditions of the environment would probably express themselves floristically in some restrictive or specialized way regardless of the history of the flora or whether or not the mountain peak had been an island.

Because islands are isolated from one another as well as from the continents, and because such isolation is often thought of as affording the most suitable conditions for speciation to proceed toward the production of endemics, it has been common practice to interpret endemism, wherever it may be found, in terms of insular history or at least to inject into it an insular connotation. I have discussed (4) some of the difficulties inherent in the concept of isolation when applied as a causal factor in endemism and have pointed out that the causes of restriction in pattern of area occupied must be sought in some environmental condition that independently occupies area.

It is significant that both on continents and on islands there occur local concentrations of endemics that seem to relate themselves to the occurrence of ions of any of several minerals which are often present in the soil solution in a concentration sufficient to exercise a restrictive effect on the vegetation through their toxicity. As a result, many of the common species of such regions are excluded from these local areas and in their places are plants that tolerate these special conditions or may even demand them. The vegetation of such areas is usually sparse and the populations of individual species are often discontinuous or localized. This condition of the environment must be closely related to some of the important causes of highly restricted patterns of distribution of plants both on islands and on continents. Of the countless thousands of seeds that chance to find their way into these toxic areas, only a very few are so constituted physiologically and genetically as to become established as functioning plants and give rise to a persistent population.

There is no evidence that the concentration and distributional pattern of endemics in continental areas has resulted from any different dynamics than such features of insular floras. In general, continental floras are larger and the mass of their species may occupy wider area, but the problems of restriction in range are identical in both. The important difference between continental and insular floras relates to problems of dispersal and establishment and the history of migration rather than to the problems of endemic restriction. Therefore, for purposes of example, it makes little difference whether we use a continental area or an insular area.

The California Flora

Certain features of the California flora, where a considerable percentage of endemism prevails and floristic diversity is closely integrated with environmental diversity, may serve to illustrate some of the problems I have discussed previously (4). Here, I think, we can clearly demonstrate the significance of certain edaphic situations in areas of endemic concentration and in addition see conclusive evidence that area in general, as occupied by species populations, is incidental to environmental conditions.

California is a region of varied relief where many complex mountain ranges and their intervening valleys lie across the path of the moisture-laden winds from the ocean. Climatically, the result is a very diverse pattern of seasonal rainfall ranging from over 100 inches annually in the northwest to less than 5 inches annually in the southeastern part of the state. Between these extremes there is no simple gradient, but a diverse pattern resulting from complications of topography that may steepen the gradient locally and produce rather sharply defined rain shadows and other similar features. Correlated with topography and rainfall is a considerable variation in seasonal and diurnal progression of temperature. Above 4,000 feet winter snows persist and seasonal dormancy prevails. Elsewhere seasonal dormancy is apt to be rather unstable as to duration and extent and to vary considerably from one species to another. In these areas, spring flowering may begin anywhere from November to March. Because of cold ocean currents along the coast and warm currents farther offshore, frequent fog, conforming to a seasonal, diurnal, and geographic pattern, envelops the maritime area. Boundaries between climatic situations often are reasonably sharp under such topographic and geographic conditions. Such a boundary would be of the nature of a steepened climatic gradient and is usually associated with some local topographic feature. The summer fog may regularly overhang a certain coast range ridge each afternoon and go no farther inland. Here the gradient of relative humidity across the coast ranges is locally steepened. The eastern boundary of the coast redwood coincides with the usual line of occurrence of such a steepened gradient. The dramatic change from upland coniferous forest to Great Basin sagebrush on the east slope of the Sierra Nevada is the expression of a steepened climatic gradient involving various aspects of the moisture relations of humidity and rainfall and ground water as these are modified by topography and drainage. The deserts, the upland coniferous forest, the foothill coniferous forest, and many other of the major floristic assemblages are all geographic expressions of the interrelationship of climate and topography and in many places are definable by rather sharp boundaries which give expression to steepened climatic gradients. Probably the best example of such a feature is the perpendicular 5,000-foot south wall of Yosemite Valley and the effect it produces on surface climate and on vegetation. Glacier Point at the top of the cliff is clothed with a red fir forest while the valley floor at the bottom of the cliff is clothed with the arid phase of the yellow pine forest. The lateral distance is but a very few feet, the vertical distance less than a mile. On a map such a boundary could only be indicated by a sharp line. I go into this detail because there are those who maintain that climatic boundaries do not exist, and that climatic features are expressible only in terms of gradients. So far as vegetation is concerned, the steepening of the climatic gradient is apt to produce an effective climatic boundary.

The edaphic variation in the area occupied by the California flora is enormously complex. There is very little in the way of cause of edaphic variation that has not left its mark in this region. A glance at the geological map of California (1) will disclose some of the outlines of this diversity as wrought by the events of geological history, but the details significant to environmental diversity are of such a nature as to defy adequate mapping. There is outlined on this map the surface occurrence of about eighty different rock systems, of which thirty-four are igneous and forty-six are sedimentary in origin. They range in age from Archean to Recent. Most of the older rock is metamorphosed. The northern California coast ranges are dominated by the Jurassic Franciscan series which taper into island-like patches in southern California. We shall return later to a discussion of this series of rock; it is sufficient here to say that they have been invaded locally by ultra-basic intrusives which are heavily serpentinized and that many other rocks of the series have also been serpentinized. The southern coast ranges are dominated by Cretaceous and Tertiary marine sediments. Most of southern California, however, is dominated by grano-diorites, undivided granites, and acid intrusives of uncertain Mesozoic and pre-Mesozoic origin. The Sierra Nevada owes its existence to the upwelling of an enormous batholith composed of various types of granite. These granites reach the Great Valley flora on their southwestern margin but are overlain by complicated Jurassic rock along their northwestern margin. To the east they are flanked by an extensive series of metamorphics. In the north they give way to volcanics. The Great Valley is recent alluvium. In the extreme northwestern part of the state, the Klamath Mountains are dominated by ancient gneissoid and schistose rocks together with very diverse types of metamorphics, volcanics, and ultra-basic intrusives. Throughout the entire California region there are local occurrences of volcanics of various types and ages and of metamorphics that are exceedingly diverse in type as well as in chemical composition. The geological map presents these rock systems each in terms of its age and general origin but in no way depicts the tremendous variation in lithology or in chemical composition which, in the case of the metamorphics and volcanics as well as in some of the older sediments, is very great.

The general correspondence of many elements of the flora of California to the distribution of lithological features is no less striking than is the above-mentioned floristic differentiation that is to be related to climatic features. Much of the diversity of the California flora results from the superposition of lithological features across the areas of special climatic conditions, thus creating local habitats that are occupied by special populations of plants. Certain of these lithological features support unusual concentrations of species of highly restricted range, thus suggesting that these plants may be particularly adapted to the special conditions present. This is especially striking in serpentinized areas where the localization of some of the ferro-magnesian metals reaches toxic concentrations lethal to many of the plants one might expect to find. Endemic restriction in California is by no means confined to serpentine areas nor is it always associated with the ferro-magnesian metals. Since these problems have not as yet been investigated from a physiological and biochemical point of view we can only postulate cause-and-effect relationships. These are problems that new techniques in biochemistry, plant physiology, and genetics have placed within our scope of investigation and beginnings are now being made toward their solution. Endemic restriction has been studied from the point of view of sterility of soils, but not from the point of view of the vegetation that flourishes in an area, an approach which may do much to solve the problem of narrow endemic restriction.

Endemism in the California Flora

It is impossible to give a precise figure as to the percentage of endemism in the California flora chiefly because of the difficulties of taxonomic evaluation of the complex groups of entities that develop under such diverse geographic conditions. Many aspects of endemism are concealed under aggregate specific categories in current usage. These often are composed of genetic races and minor variations with special habitat adaptations, which, if carefully depicted, might aid considerably in solving the complex problems of endemism. There are few if any of the major divisions of the California flora that do not have some element of highly restricted endemism in their population. This may also be said of the major topographic features. Jepson (2) records about forty per cent endemism for the California flora. Most of the valid species described for this area since the appearance of Jepson's "Manual" are endemic, so that this figure must be raised considerably. There are also extensive sections of the state that have not been adequately explored and, since these regions are chiefly areas of great edaphic diversity, it is to be expected that several more species will be added to the known flora.

Jepson (2) noted that local endemic species in California seemed to be aggregated into definite areas. He interpreted these concentrations as comprising ten such areas, three of them in insular and southern California and seven in northern California. Since we intend to demonstrate that area is incidental to environmental condition, we need not go into the matter of the adequacy or inadequacy of their number and distribution. Although his discussion is meager, in his interpretation Jepson points to the classical concept of relict and recent species and emphasizes age and history of land mass, particularly with respect to its elevation and subsidence. He leans strongly on the concept of "mountain top" endemics and refers broad endemics to climatic features of the region. Although his "Franciscan area" conforms to the areal pattern of much of the Franciscan lithological series of northern California, he makes no mention of any lithological relationships. Detailed discussion of a part of one of Jepson's endemic areas will serve to illustrate the main points of the present paper.

The Napa-Lake Area

In northern California, Napa and Lake counties are designated by Jepson as his Napa-Lake endemic area. We will consider a portion of this area involving southern Lake County and northern Napa County and the adjoining margins of Sonoma, Colusa, and Yolo counties (fig. 1). This area is approximately thirty miles square and manifests marked floristic diversity and richness as well as considerable endemic concentration. In addition there are many species of special habitats that recur elsewhere only where such special habitats reappear in the coast ranges or in the Sierra Nevada foothills. In this small area there outcrop no less than sixteen distinct geological series, ranging from sedimentary rock of Jurassic and Cretaceous origin to Recent alluvium; metamorphic rocks of both igneous and sedimentary origin, some of which are highly serpentinized; volcanics involving basalt, rhyolites, tuffa, and obsidian, ranging from unclassified Tertiary in age through Pliocene, Pleistocene, and Recent time; and finally a considerable expanse of ultra-basic igneous intrusives which have been highly serpentinized. Commercially exploited minerals of the region are mercury, gold, silver, and sulphur. Hot springs and mineral springs are common. The geological outcrops form the surface pattern of the high relief and one finds the usual habitat features to be expected in mountains. Several streams traverse the region and Clear Lake penetrates about one-fourth of the way through the area from the northwest. Several small lakes and ponds, ranging from very alkaline to highly acid in character, occur within the area. Some of them, such as Borax Lake, are almost entirely devoid of marginal vegetation, while others, like Boggs Lake, possess a rich marsh flora in floating bogs. In the playas and the alluvial meadows that are common throughout the region there is evidence of many more lakes of past time.

The outstanding geological feature of this area, aside from its local diversity, is the fact that it is dominated by a basement of metamorphosed Franciscan rocks of Jurassic age which have been invaded in many places by ultra-basic intrusives. The Franciscan rocks themselves have become serpentinized in many places; in others, their dominant ferro-magnesian character makes them the habitat of a peculiar flora. These Franciscan rocks are so important to the problem of endemism in northern California that it is necessary to emphasize their nature. They are the dominating feature of the geology of the northern California coast ranges. Reed, in the "Geology of California" (6, p. 29) says, "The Franciscan series may with almost equal propriety be considered 'blanket' or 'basement.' It consists of a complex series of sediments and interbedded or intruded igneous rocks of peculiar types. Equally peculiar metamorphic rocks are associated with them in many places. In some regions the latter are limited to the contacts of the igneous and sedimentary rocks; in others they constitute the whole series over large areas.

"An important constituent of most Franciscan areas is serpentine, derived from peridotite and similar basic rocks. Partly because of the prevalence of this rock, the series as a whole yields to deforming forces much more readily than the Granitic Basement. Extreme complexity of structure is almost a distinguishing feature of the Franciscan. Where it is overlain even by a thin cover of sediments, the latter also yield easily to deforming stresses. Folds of many types and sizes are therefore characteristic of areas underlain by the Franciscan."

The Franciscan is characterized by a considerable diversity of lithology. Of sediments there are conglomerates, sandstone, shale, variegated chert, limestone, and a small amount of coal. The igneous series includes schist, basalt, diabase, peridotite, pyroxinite, and gabbro; these latter are usually serpentinized. The metamorphics may be quartz schist, quartz albite schist, prasinite, blue schist, talc rock, or serpentine rock. Unfortunately, the geological map of California does not differentiate the lithological types within the Franciscan, and hence does not give an adequate idea of the lithological diversity of any area dominated by the Franciscan series. Not all of these lithological types will be found within the area under discussion, but a sufficient variety exists to add materially to the edaphic diversity of the region. Of special interest is the series of basic metals usually associated with the Franciscan, particularly where it has been serpentinized. Many of these metals become ionized in the soil solution in quantities sufficient to be lethal to many plants and are an important factor in the sterility of soils derived from such rocks (7). These metals comprise the ferro-magnesian complex and include, in addition to iron and magnesium, considerable quantities of chromium, manganese, nickel, and titanium. Whether or not titanium plays any role in the restriction of plants is not known; it is a matter of interest, however, to note its presence in considerable quantities in nearly all Franciscan rocks. The important feature of the occurrence of these metals and minerals to our thesis is the fact that they are not distributed uniformly throughout the serpentines but occur singly or in groups of various composition in local surface areas in contrast to other surface areas of differing composition and concentration.

It should be evident from this very brief discussion of the out-

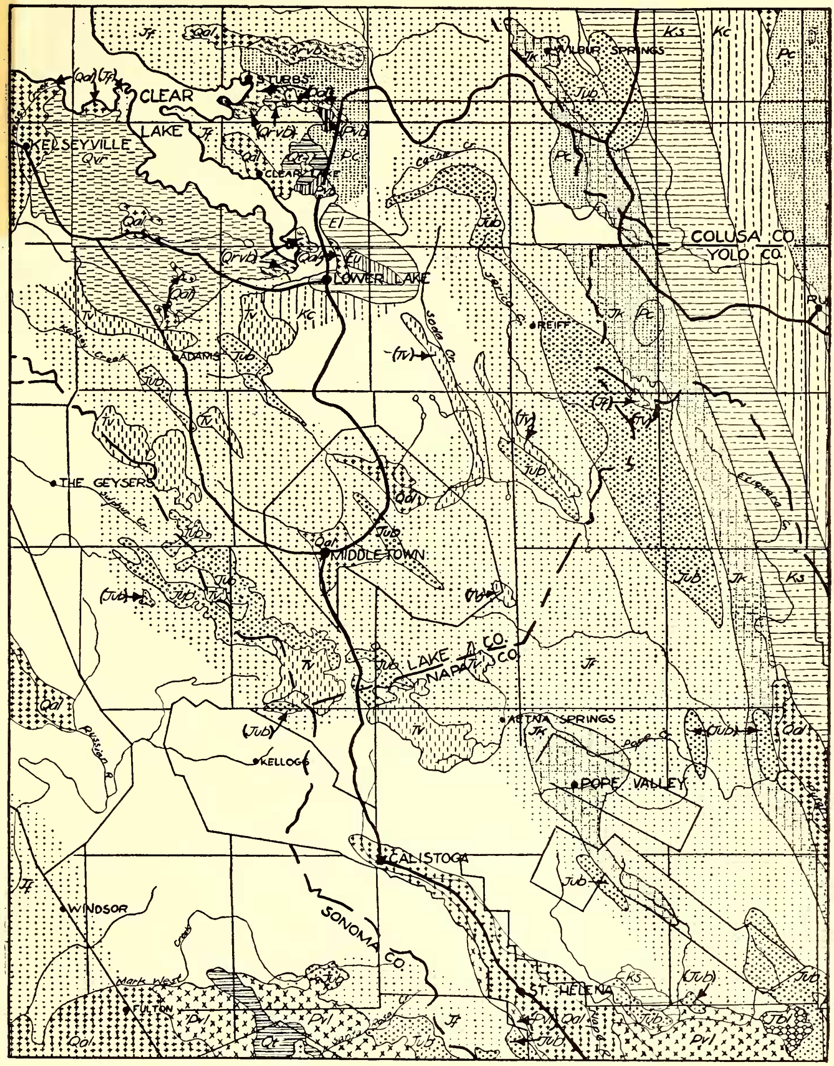

FIG. 1. Geology of the Napa-Lake Area. *El,* Lower Eocene marine sediments; *Eu,* Upper Eocene marine sediments; *Jbi,* Jurassic basic meta-igneous rocks; *Jf,* Franciscan group; *Jk,* Knoxville formation; *Jub,* Jurassic ultra-basic intrusives; *Kc,* Upper Cretaceous marine sediments; *Ks,* Lower Cretaceous marine sediments; *Pc,* undivided Pliocene non-marine sediments; *Pvb,* Pliocene basalt; *Pvl,* Lower Pliocene volcanics and interbedded sediments; *Qal,* alluvium; *Qrvb,* Recent basalt; *Qt,* terrace deposits; *Qvr,* Pleistocene rhyolite; *Tv,* undivided Tertiary volcanics; *clear areas,* unmapped geology and lakes. Adapted from O. P. Jenkins, Geologic Map of California, 1938.

standing geological features that this is a region not only of high edaphic diversity, but that this diversity embraces rocks of peculiar types, rich in minerals that are restrictive to many plants and to which other plants may have been adjusted through genetic processes involving tolerance. When one adds to this the complicated climatic mosaic, characteristic of mountainous sections in arid regions, some idea may be obtained of the tremendous environmental diversity that prevails in this very small area.

Floristic Diversity

In response to such environmental diversity, the flora of this area, in spite of its local paucity on certain very extensive "barrens," is so diverse as to total an inordinately high number of species for so small an area. More than one thousand species of spermatophytes and ferns are known here, or about one out of every four of the species listed in Jepson's "Manual." In other words, one-fourth of the species of the flora of all of California is found in this area of only thirty square miles. This is not so surprising when it is realized that the eastern extension of the redwood forest reaches this area; both the upland and the foothill coniferous forests are represented; the "black oak–madrone" forest, the valley oak meadows, and several distinct types of chaparral occur here. Except for certain types of chaparral and the oak-covered hills, none of these floral assemblages really typify the area. However, some of them may have been more extensive in the not-too-distant past, for on every hand there is evidence of repeated fire. In prehistoric times this was the home of a large Indian population which used burning in its program of game management.

Looking at the floristic diversity from another point of view, we find that of the thirty species of conifers reported from north of San Francisco Bay, twelve occur here, yet the area is only locally clothed with coniferous forest and one normally thinks of this region as being outside the coast range coniferous belt. Of the fifteen species of oaks recorded in California by Jepson, ten occur here. The genus *Navarretia,* comprising twenty-nine species in western North America, has eighteen species in this area, seven of which are restricted to this locality or occur elsewhere only in one or two isolated spots. Of the forty-four species of *Ceanothus* in California, ten occur here. Of the ten species of *Linum* in California, seven occur here. A large number of serpentine endemics find their way into this area, but endemism within the region is by no means confined to the conditions prevailing in serpentine.

Endemism in the Napa-Lake Area

Although an impressive number of species and smaller taxonomic categories occur in this area and are not known outside of it, none of them conforms to the pattern of the whole area but rather to the pattern of certain localized conditions that prevail within the area. Furthermore, a large number of the peculiar plants of the region occur discontinuously throughout the area on special habitats and recur beyond in one or more places on similar habitats only. Most of these habitats involve peculiar rock types. The uniformity of this coincidence of restricted endemism and peculiar environments suggests that these plants owe their distributional pattern to the configuration of the pattern of edaphic conditions. To these conditions they are physiologically adapted through the processes of genetics and evolution. Of the particular environments within this area wherein restricted endemics are found, three are outstanding. Most striking are those associated with the various local conditions that prevail within the chemical structure of serpentine and its various mineral associates. Next, are those associated with conditions prevailing in association with the volcanics. Finally, there are the conditions prevailing in the vernal pools and other similar habitats wherein the ground is covered with water during the establishment phase of the seedlings, while flowering and fruiting of many of the species population takes place only under conditions of extreme drought. There are endemics in other situations as well, but the spectacular concentrations are manifested in these three situations.

Endemism in the serpentine areas presents the most complex problems. Here the distribution patterns of the various serpentine endemics range from (a) species that are general to serpentine practically wherever it occurs in the California area through (b) species that are discontinuous on the serpentine, to (c) species that are known only from one small locality or niche in a given serpentine area. *Quercus durata* is fairly common over most of the serpentine areas of the northern California coast ranges; *Cupressus Sargentii* is highly discontinuous on serpentine, although it is known from southern California (Santa Barbara County) to southern Oregon; *Collomia diversifolia* is known from only four localities, three in the Napa-Lake area and one in the Mount Hamilton Range. A few species, like *Linum bicarpellatum,* are known from but a single locality; but their number is very small, and is no more spectacular in the Napa-Lake area than in any of several other serpentine districts. Most significant to our problem is the fact that many of these supposedly highly localized Napa-Lake species are being found on similar serpentine outcrops elsewhere as a result of more thorough exploration. We now know several of these endemics to occur in the Red Mountains of the Mount Hamilton Range (8) and another series of them to occur in the serpentines of the foothills of the Sierra Nevada in Eldorado County. This seems to be pretty clear evidence that we are dealing with environmental conditions rather than with any of the spatial or historical attributes of area. Aside from the fact that the rocks in the different sites on which these plants are growing are all of Jurassic age, their precise histories subsequent to that time have varied. They have in common similar chemical composition and occur in similar climates. Although the species of the area must be in tune with climate, climate may be ruled out as a cause of their narrow restriction because in all of these areas, adjacent rock masses in apparently identical climates have not proven suitable habitats for these species. We are left with the condition of edaphic factors, either water relations of the substratum or the chemical and physical character of the soils and soil materials. Localization on serpentine is often very narrow. *Linum bicarpellatum* occupies only a few hundred square feet. The area occupied by *Collomia diversifolia* in each of its occurrences is even smaller. Both of these species occur where vegetation is sparse and competition does not appear to be a factor. Often a group of individuals will occur in a situation completely devoid of any associated vegetation; outside of this one colony the soil is naked. Clearly it is not competition with other plants that restricts such species. Their behavior suggests the presence of toxic substances in the soil or perhaps the absence of some critical substance. It is significant that certain genera, such as *Linum, Navarretia, Streptanthus,* and *Astragalus,* show a marked tendency toward taxonomic elaboration in the presence of local aspects of serpentine.

The volcanics of this area likewise possess a considerable population of endemic species and of species occurring discontinuously elsewhere under similar conditions. Aside from the broad lithological classification, nothing is known as to the nature of metals that may be local in any rock or soil type. The close proximity of some of these outcrops to the Jurassic ultra-basic intrusives would make some infiltration of ferro-magnesian metals inevitable. In addition, the basalts are by nature highly charged with ferro-magnesian metals. Most conspicuous among the habitats of peculiar plant species of this area, however, is a matrix made up of volcanic ash and obsidian rubble. Unlike the serpentines, it is fairly rich in species of plants. The surface layers of the soil become excessively dry during the summer so that herbs are less common than shrubs, but these few herbs comprise most of the endemics in these conditions. That the problem is related to the ferro-magnesian metals is suggested by the occurrence of several highly discontinuous species, such as *Eriastrum Abramsii,* which in some other localities is on serpentines but is not as yet known on any of the local serpentines of the Napa-Lake area. This may be a dangerous conclusion because of the possibility that in this case we may be dealing with distinct ecotypes of the species adapted to a special condition in all of its various localities.

The third condition of concentration of endemics is the vernal pools and other habitats where water stands in spring and extreme drought frequently prevails in summer. Here the problem varies with the particular lithology, since similar water conditions occur in conjunction with serpentine, volcanics, adobe clay, and the margins of peat bogs. It is in these habitats that the genus *Navarretia* of the Polemoniaceae is undergoing elaborate speciation. Three closely related species occur respectively in adobe clay, the volcanics, and on the margins of a peat bog. Distinct color forms of one of the species occur in two ponds less than a mile apart; in one pond the plants are white-flowered, in the other, light blue. Locally, on the margin of the blue colony, a dark, blue-flowered strain appears to be developing. These vernal pool plants begin their life history submerged. The leaves are linear-terete; the hypocotyl develops a thick cortical layer made up of very large air cells. As the water recedes and the soil dries the new growth becomes rigid and the leaves and bracts become spinose dissected. At flowering time the soil is usually deeply cracked and dry. Species of several genera undergo a similar growth history in these pools. Most spectacular is the genus *Eryngium* of the Umbelliferae, whose aquatic phase possesses floating leaves and whose arid phase is exceedingly spinose. There are, on the other hand, other plants that complete their life cycle before the land becomes excessively dry. Among these are the species of *Downingia* (Lobeliaceae), many of which are endemic to vernal pool conditions in California; one is endemic within the Napa-Lake area. These vernal pools present complex problems with respect to rate of water recession and hydrogen-ion concentration as well as to the mineral constituents of the water and the soil solution. Obviously the boundary of the pool presents one limiting factor to the spread of these plants. However, within the water conditions common to all of the pools, there is evidence from the differences in the floras that other edaphic factors are operating and have operated long enough to have selected several local endemic types. Some of these endemics at present are known only from single pools; in these pools they are often very abundant.

Within the Napa-Lake endemic area of Jepson, there is apparently ample evidence that the endemism is to be related in most instances to edaphic conditions and that the area as outlined by Jepson is of significance only because it contains several different edaphic situations on which endemics have developed. Strictly speaking, however, these conditions in most instances overstep the boundaries set by Jepson, and often widely so. However, whether these conditions occur within or without the area they are almost always very localized.

Taxonomic Aspects of Certain Endemics

Considering these problems from the point of view of taxonomic relationships and comparative distributional patterns of closely related forms, we can arrive at more corroborative evidence to support the general thesis that distributional pattern is the direct result of environmental condition, and that the edaphic factor is most apt to be responsible for highly restricted patterns of distribution. It is important to emphasize at the outset that very little is known about cause-and-effect relationships between taxonomic entities and any environmental conditions to which they may seem to be adapted. It is, however, equally important to call attention to cases where consistent occurrence in a given situation suggests that a relationship exists between the conditions prevailing in the habitat and the physiological and genetic makeup of the plant, even though we cannot state precisely what the nature of that relationship may be. For illustrative material of these relationships I have selected a varied group of plants, some of which belong to genera containing several species with apparent restrictive adaptations to environmental conditions; others are single localized species isolated from a widespread closely related species by adaptation to a peculiar habitat; still others may be only genetic races within a species, which show restrictive habitat preferences not shared by the species or its normal associates in other situations.

Libocedrus decurrens is a common member of the upland coniferous forest of the Sierra Nevada. It occurs normally with *Pinus ponderosa* and *P. Lambertiana* chiefly on soils associated with granitic rocks. In the northern Sierra Nevada, however, where much serpentine prevails, it is predominantly a serpentine inhabitant; in the Napa-Lake area of the North Coast Ranges it is confined to serpentine. Both of the species of pines associated with *Libocedrus decurrens* in the Sierra Nevada occur also in the Napa-Lake area. Although in one outstanding situation in the Napa-Lake area, where the geological contact between the serpentine and adjacent rock passes between a colony of *Pinus Lambertiana* and one of *Libocedrus decurrens,* the pine does not occur over the contact on the serpentine and the *Libocedrus* does not occur off the serpentine. *Pinus ponderosa,* on the other hand, occurs on both sides of the contact. We are dealing here with what appear to be cases of selective tolerance. The main Sierra Nevada race of *Libocedrus* is adapted to granitics; the race of the North Coast Ranges is a serpentine endemic. Apparently mixed populations occur in the northern Sierra Nevada, but the non-serpentine race is less common than the serpentine race. *Pinus Lambertiana,* although known from several rock types, does not tolerate serpentine. Such differences in tolerance, where they characterize whole populations, must be interpreted as resulting from genetic processes whether they involve whole species or only races within species.

Collomia diversifolia, a serpentine endemic of very localized occurrence, is known from two localities in Lake County and one in adjacent Colusa County. It was believed to be a Napa-Lake endemic until Mrs. Sharsmith (8) found it in the Mount Hamilton Range in Santa Clara County. It is closely related taxonomically to the widely ranging *C. heterophylla,* which is known from many diverse types of soils including some serpentine. It is not known, however, from the heavy ultra-basic intrusives such as those on which *C. diversifolia* occurs. Here, again, it seems obvious that the genetic forces that operated to set these two species apart, acted upon physiological as well as morphological characters with the result that so long as each retains its present physiological and genetic constitution, the geographic area of the one will be separate from that of the other.

Among genera most conspicuous for their endemic species in the California flora is *Navarretia.* Within the Napa-Lake area speciation has proceeded along very interesting lines in different groups of the genus. In vernal pools not more than four or five miles distant from one another occur *N. Bakeri, N. pleiantha,* and *N. pauciflora* (3), all close relatives of *N. leucocephala* of the Great Valley and of *N. prostrata* of southern California. Their morphological features, particularly with respect to stamen insertion, suggest that a relationship with *N. prostrata* is closer. Their floral structures, with minor exceptions of size and color of corolla, are identical; the chief differences are in the inflorescence, the bracts, and the habit of the plants. They, however, show striking ecological preferences: *N. Bakeri* occurs in vernal pools in adobe soil in oak-grassland; *N. pleiantha* occurs on the margin of an acid bog in soil very rich in organic materials; *N. pauciflora* occurs in a playa in volcanic ash heavily strewn with obsidian rubble. All of these species begin their life cycles as aquatics and mature as extreme xerophytes. Speciation apparently has proceeded here along lines dictated by edaphic conditions. The genetic diversity evident in the plants of any particular pool does not appear very great. This may, however, be more apparent than real. Genetic diversity here is probably masked by rigid habitat selection, but such diversity will soon disappear as a result of random fixation unless some agency for gene infiltration from other habitats is operative.

Another set of closely related species involves *Navarretia Jepsonii, N. mitracarpa,* and *N. Jaredi. Navarretia mitracarpa* must be ruled out of our discussion because it has been collected only once from "somewhere in Lake Co.," and we do not know under what conditions it grows. *Navarretia Jaredi* exhibits considerable local variation on serpentine and other ferro-magnesian rocks of the South Coast Ranges. It is not, however, an inhabitant of vernal pools. *Navarretia Jepsonii,* a plant of vernally wet habitats and for the most part aquatic in its seedling stages, is confined to highly serpentinized ultra-basic intrusives. Its chief claim to distinction is a doubled number of capsule valves and the membranous character of the matured capsule. Morphologically *N. mitracarpa* forms a connecting link between *N. Jepsonii* and *N. Jaredi.* Here, again, is a case of speciation involving both morphological and physiological characters and exhibiting differences in geographic restriction.

A third case in the genus *Navarretia* is that of *N. eriocephala* occurring on ultra-basic intrusives in Lake, Solano, and Colusa counties in the North Coast Ranges and across the Great Valley in Eldorado County on similar rock. This discontinuity is clearly related to the nature of the edaphic conditions.

The distributional patterns of the members of the genus *Cupressus* are likewise of such a nature as to suggest a close relationship with edaphic conditions. In the Napa-Lake area both *C. Macnabiana* and *C. Sargentii* occur. Both are confined to serpentine and grow together at many places in the inner North Coast Ranges. *Cupressus Sargentii* occurs in highly localized spots as far south as Santa Barbara County, and extends into the outer coast ranges. *Cupressus Macnabiana* occurs both farther north and eastward than does *C. Sargentii.* The fact that these two plants grow together in parts of their ranges suggests that they can tolerate certain conditions in common. Their restriction must be related to different causes. We must not rule out the possibility that we may be dealing with distinct ecotypes in the various habitats. Closely related to *C. Macnabiana* are *C. Bakeri* of the Modoc lava beds and *C. nevadensis* from igneous rocks near Bodfish, Kern County. Since lavas are often rich in ferro-magnesian minerals we find here a thread of consistent edaphic pattern for the speciation in this group of closely related species. Likewise, *Cupressus macrocarpa, C. Goveniana,* and *C. pygmaea* occur on grano-diorites which are similarly rich in ferro-magnesian minerals. Possibly speciation throughout the genus *Cupressus* has followed a closely related edaphic pattern of environmental restriction.

The genus *Streptanthus* (5) is replete with serpentine endemics. Of nineteen species in California, eleven are confined to serpentine or other closely related ferro-magnesian rocks: *S. Breweri* occurs through the middle and inner coast ranges from Tehama County to San Benito County; *S. glandulosus* ranges from Colusa County to San Luis Obispo County; *S. polygaloides* occurs along the northern Sierra Nevada foothills; the remaining eight species are exceedingly local in their occurrences, some being known only from single localities, ranging from serpentine outcrops in the mountains of San Benito County to the ultra-basic intrusives of Lake and Colusa counties. *Streptanthus* is another genus in which speciation has been concerned with selective elaboration over the edaphic environment.

Summary

Consideration of these endemics in terms of any specific local area soon makes one aware that many of them exceed the limits

of the area and recur elsewhere in similar edaphic situations. These facts serve to emphasize the importance of environmental condition over area particularly where area is delineated on some historical or supposedly historical basis. It is obvious that the Napa-Lake area owes its high concentration of endemics to its great edaphic diversity and especially to the fact that this diversity involves peculiar rocks and their associated minerals. Next in order of importance is the presence in the area of a number of genera capable of elaboration over these peculiar habitats. Those genera which give rise to an occasional endemic species are not responsible for the large number of endemics. It is, on the other hand, such genera as *Navarretia, Linum,* and *Streptanthus* which develop many local species and habitat races, that build up the population of restricted endemics in a small area and that give the impression of some sort of genetic instability. It becomes clear that diversity in the environment must work with genetic diversity and must involve diverse tolerances, to produce situations such as that in the Napa-Lake area or in any rich floras. The paucity of a flora will reflect a failure of some aspect of this diversity. The localization of the area of any of the members of such floras is purely an expression or indicator of habitat conditions. The significant configuration of area is that which coincides with environmental conditions as these involve presence or absence or degree or amount, or as area may be delineated by the extremes of some critical conditions.

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